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Late Tertiary Mammals from the Mongolian People's Republic¹

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ABSTRACT

Age assessment of Late Tertiary rocks north of the Altai Mountains, Mongolian People's Republic, is refined by renewed study of a small collection of mammalian fossils made by the Central Asiatic Expedition in 1925. A dentary fragment with P₃ assignable to *Trischizolagus* most closely resembles an early Pliocene member of the genus from Afghanistan. *Trischizolagus* is also known from late Miocene and Pliocene deposits of Spain, France, Romania, and Greece. An equid, formerly

considered as Equus and an indicator of Pleistocene age, is a hipparionine referable to "Hipparion" housenesse. Other elements of the fauna are "Oioceros" sp., a proboscidean possibly representing Sinomastodon, and a rhinocerotid resembling Chinese Chilotherium. All are comparable to Late Tertiary taxa known from elsewhere and suggest an age for the sediments near the Miocene-Pliocene epoch limit.

INTRODUCTION

Review of the small mammals collected in Shanxi Province, China, during the 1930s by the Frick workers Kan Chuan Pao (Buckshot) and Liu Hsi Ku, led to examination of material found during the earlier Central Asiatic Expedition to Outer Mongolia. These two fossil hunters had been members of that series of field crews in the 1920s. Several specimens found by Walter Granger's field party in 1925 come from young rocks lying on fossiliferous Oligocene deposits north of the Altai Mountains (fig. 1). These deposits now appear to be close in age to some of the Late Tertiary Shanxi localities.

- ¹ Publications of the Asiatic Expeditions of the American Museum of Natural History, Contribution No. 165.
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One fossil is a representative of the Leporidae, a lagomorph family not commonly represented in collections from Mongolia, but represented by Alilepus at Ertemte, Inner Mongolia (see Fahlbusch et al., 1983). Previously, Dr. M. R. Dawson (1961) had analyzed Late Tertiary ochotonids from Inner Mongolia. The Mongolian fossil rabbit is unlike any specimen so far recovered from China, but it resembles fossils from Afghanistan and the Mediterranean. Affinity may also lie with Late Cenozoic Serengetilagus from Africa and with extant Lepus. By contrast, an equid from these deposits is clearly referable to a Late Tertiary hipparionine species from northern China. The assemblage argues for greater antiquity of these deposits than was previously suspected.

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ABBREVIATIONS

AFG, Numbered specimens from Afghanistan cataloged by the Institut de Paleontologie, Museum National d'Histoire Naturelle, Paris.

AMNH, Numbered specimens of the American Museum of Natural History, New York.

BM(NH), Numbered specimens of the British Museum (Natural History), London.

KNM-KW, Numbered specimens from the local-

ity Kanam West, which are accessioned at the Kenya National Museums, Nairobi.

PMU, Numbered specimens of the Palaeontologiska Museet of the University of Uppsala, Sweden.

RV, Numbered specimens of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

THP, Collections of the Tianjin Natural History Museum, Tianjin, China.

COLLECTING BY THE CENTRAL ASIATIC EXPEDITION

In the summer of 1925, the Central Asiatic Expedition of the American Museum of Natural History camped on the shore of the playa Kholobolchi Nor, north of the Altai Mountains in north central Outer Mongolia (fig. 1). Relatively undisturbed buff to gray colored beds cropped out around the camp at about 45.5°N 101°E (Andrews, 1932; Osborn, 1930). Superposed on older deposits assigned to the Hsanda Gol Formation, these sediments seemed homogeneous to the field party, and were named collectively the Khunuk Formation. The Khunuk Formation has been believed to be considerably younger than the Hsanda Gol Formation, i.e., usually Pleistocene (Berkey and Morris, 1927, p. 385). Kholobolchi Nor and the neighboring Khunuk Valley to its east are some 30 km west northwest of Hung Kureh, a region richer than Kholobolchi Nor in vertebrate fossils, including abundant hipparionines, and considered pre-Pleistocene (Osborn, 1930; Berkey et al., 1929; fig. 1 here).

The following short history of collecting is compiled from fieldnotes of Drs. W. Granger and F. K. Morris and a statement by Granger in Osborn (1936, p. 397). On June 29, 1925, "about 5 miles" east southeast of their camp, a lower jaw fragment of a horse with P₂-M₂ was found and identified as "Equus" by Granger. This specimen occurred low in a section "120 feet" thick, and other fossils lay scattered "on both sides of the trail." It is this specimen that resulted in an erroneous indication of Pleistocene age (see below). On July 1, "5 to 8 miles north" of this site, a single fossil was found in a separate outcrop. This specimen, AMNH 21615, was made the holotype of Serridentinus florescens by Osborn (1929), but is considered indeterminate herein.

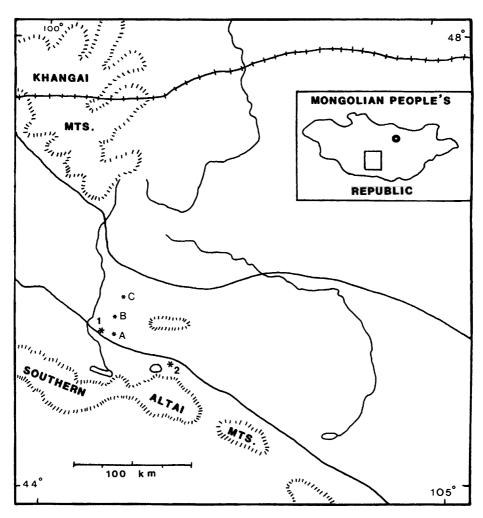


Fig. 1. Map of area north of the southern Altai Mountains, showing the Kholobolchi Nor camp site (1) and Hung Kureh (2). The small stars A, B, and C approximate the three collecting areas in the Khunuk Formation of the 1925 field party; they coincide with the Khunuk Valley indicated by Osborn (1930). Three stream beds are shown, two of which end in small ephemeral lakes; a third lake near Hung Kureh is Tsagan Nor. The inset shows the mapped area of the People's Republic of Mongolia. Map adapted from Andrews (1932) and Osborn (1930).

On July 8 and 9, 1925, a third set of exposures (thinner, about 10 m) of Khunuk Formation was investigated. These deposits, "about 15 miles northeast of camp," yielded a number of fossils, including a leporid, a bovid horn core, and a fragmentary rhinocerotid premolar described below. To maintain integrity of original collecting data and the possibility that the three localities could be different in age, the collecting sites of June 29, July 1, and July 8 and 9, 1925, are designated as Kholobolchi Nor A, B, and C, respectively (see fig. 1).

SYSTEMATICS

ORDER LAGOMORPHA BRANDT, 1855 FAMILY LEPORIDAE GRAY, 1821

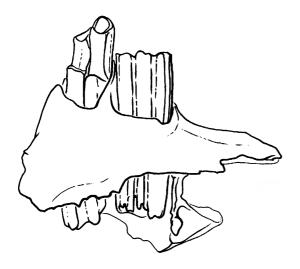
Trischizolagus Radulesco and Samson, 1967

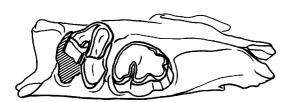
Trischizolagus sp.

REFERRED MATERIAL: AMNH 21617, right dentary fragment with broken P₃ and P₄.

LOCALITY AND HORIZON: Kholobolchi Nor C; strata assigned to the Khunuk Formation.

DESCRIPTION: The partial right dentary





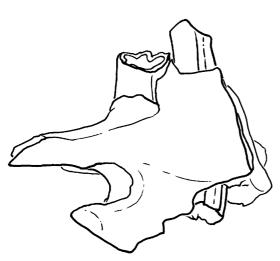


Fig. 2. Three views (top to bottom: lingual, occlusal, labial) of AMNH 21617, *Trischizolagus* sp.

bears a P₃ that is broken cleanly on a horizontal plane so that the enamel pattern is

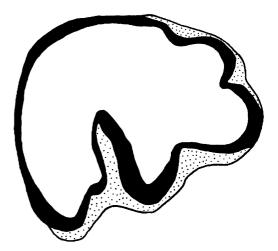


Fig. 3. Occlusal view of P₃ of AMNH 21617, *Trischizolagus* sp. Solid black indicates enamel; stippling represents cementum.

clear, and a shattered P_4 that includes a portion of its original wear surface (figs. 2, 3). The fragmentary dentary includes the base to the alveolus for the lower incisor on the medial side, just anterior to P_3 , at the midlevel of the jaw.

 P_3 (length = 3.30 mm, width = 2.84 mm) has a deep posteroexternal reentrant (hypoflexid) and three shallower indentations. The pattern reproduced in figure 3 is taken from the surface of the 10 mm high broken tooth. The hypoflexid reaches about halfway across P₃ and there is no internal fold (posterointernal reentrant, or mesoflexid) opposite to it. The enamel of the walls of the hypoflexid is not crenulated. The posterointernal corner of P₃ is rounded smoothly. Of the three smaller anterior folds, the anteroexternal reentrant is the deepest. All three folds persist to the base of the crown. Cement covers the external side of P_3 and is thinner anterointernally. There is a narrow anteroexternal vertical strip on P₃ that lacks cement. The posterior and posterointernal walls of the tooth lack cement also.

The talonid of P_4 is smaller than the trigonid (trigonid width = 3.53 mm, talonid width = 3.01 mm, P_4 length = 2.88 mm). Crown height from the wear surface is 13 mm. Externally, the trigonid and talonid are rounded rather than angular.

DISCUSSION: The Kholobolchi Nor leporid

shows the characteristic P₃ trigonid of *Trischizolagus*, with three folds in anterior, anteroexternal, and anterointernal position. The posteroexternal reentrant (hypoflexid) of AMNH 21617 is not as derived as in most living leporines where it traverses nearly the entire width of the crown and particularly in *Lepus* and several other genera, in which the posterior wall of the hypoflexid is crenulated (see Lyon, 1904, pp. 352–353 and pl. 91). *Lepus* and *Sylvilagus*, which cannot be distinguished by premolar morphology (White, 1984), lack a posterointernal reentrant (mesoflexid).

Trischizolagus is known from the late Neogene of Romania, Spain, France, Greece, and Afghanistan. Radulesco and Samson (1967) based the type species of the genus on late Pliocene material from Malusteni and Beresti in southern Moldavia. Most individuals of their species, Trischizolagus dumitrescuae, possess a mesoflexid, which is always smaller than the hypoflexid. The late Miocene T. crusafonti (Janvier and Montenat, 1970) from La Alberca, Spain, originally considered to constitute a new genus Hispanolagus, is transferred to Trischizolagus by Lopez-Martinez (1977; see also Sen, 1983). The two known P₃'s of this species have a short mesoflexid and the specimens are smaller than average size for T. dumitrescuae.

The sample of Trischizolagus maritsae de Bruijn et al. (1970) from Maritsa, Greece, shows variation in development of the mesoflexid on P₃. The reentrant in this late early Pliocene species is of variant vertical depth and size and is absent in two worn specimens. De Bruijn et al. (1970) postulate that T. maritsae is primitive in its inconstant development of the mesoflexid, with respect to T. dumitrescuae, in which the mesoflexid is usually present. T. maritsae is also considerably smaller than the latter species. T. maritsae from Roussillon, France, may be about the same age as the Greek sample, but details of the dentition are still under study (Mein and Aymar, 1984).

Sen (1983) described *Trischizolagus* from Pul-e Charkhi, an early Pliocene site in Afghanistan. His sample included two worn P₃'s, one of which preserved only an islet remnant of the mesoflexid. The other tooth lacked a mesoflexid. Sen (1983) named the sample

Trischizolagus cf. maritsae [sic], mentioning several differences from the Maritsa sample.

The Kholobolchi Nor Trischizolagus most closely resembles the sample from Pul-e Charkhi. In both AMNH 21617 and AFG 759, the mesoflexid is absent, such that the surface of the tooth is rounded posterointernally. The hypoflexid walls are uncrenulated. The teeth are of about the same size, clearly larger than those of T. maritsae. For this reason and others cited by Sen (1983), these specimens are not assignable to T. maritsae and may represent the same new species. A new taxon is not diagnosed here for lack of more complete material.

Among other known Late Tertiary leporids from eastern Asia, those from northern China do not resemble AMNH 21617. From the Yushe Basin, Alilepus annectens is well represented, and its P₃ differs from that of Trischizolagus in possessing a strong mesoflexid that persists throughout wear and in having a smoother trigonid that lacks an anterior reentrant and sometimes also the anterointernal reentrant. P₃ of Asian Hypolagus is simpler, having a weaker mesoflexid and lacking the anterointernal reentrant in all specimens. True Lepus is also represented in China. Caprolagus sivalensis, from the Siwalik Hills, India, as represented by BM(NH) M16529, is probably correctly assigned at the generic level on the basis of its complex P₃ with expanded trigonid bearing two or three narrow anterior reentrants, as well as anteroexternal and anterointernal folds. Pliopentalagus is similar (see Daxner and Fejfar, 1967); however, this genus has both a hypoflexid and mesoflexid, whereas in Caprolagus the hypoflexid traverses the tooth.

As concerns North American leporids, *Paranotolagus complicatus* Miller and Carranza-Castaneda, 1982, most resembles AMNH 21617 in location of reentrants on P₃, but all figured specimens have complicated enamel and an inflated, labyrinthic anterior internal reentrant.

Trischizolagus shares similar P₃ trigonid morphology with a Late Cenozoic leporid from Africa. For example, AMNH 21617 is similar to an undescribed leporid left P₃, KNM-KW 138, from the Pliocene East African locality Kanam West in Kenya. These specimens are about the same size and both

lack a mesoflexid. Anteroexternal, anterior, and anterointernal reentrants are developed similarly. However, KNM-KW 138 has a shorter trigonid and a deeper hypoflexid that passes the midline of the tooth.

This specimen (KNM-KW 138) may be referable to Serengetilagus Dietrich (1942), which is represented by good suites of material from several Pleistocene localities. These samples show variation among individuals that can be used in interpreting relationships of the genus. MacInnes (1953) showed that the anterointernal reentrant in the P₃ of Serengetilagus is not present in all specimens and that the mesoflexid (although he did not recognize it as such) occurs rarely in Serengetilagus praecapensis.

The differences between Serengetilagus and Trischizolagus are mainly in the frequency of occurrence of reentrants on P₃, rather than their presence or absence. Perhaps of greater significance is the presence of more cement on P₃ in AMNH 21617 than is apparent on available casts of Serengetilagus or on specimens figured by MacInnes (1953). If future work shows that these traits are not definitive, then Trischizolagus should be considered a junior synonym of Serengetilagus.

Comparison of species of *Trischizolagus* and Serengetilagus praecapensis suggests that a trend toward reduction and loss of the mesoflexid occurred in this leporid group. Spanish Miocene Trischizolagus usually shows a mesoflexid; Pliocene species show it occasionally; and Pleistocene Serengetilagus has it rarely. The exception to this progressive transformation is the late Pliocene Romanian species, which usually retains the mesoflexid. If the polarity of mesoflexid depth is toward its reduction, then Serengetilagus praecapensis would be a late, derived member of this group. This trend contradicts the hypothesis of de Bruijn et al. (1970) that follows from evaluating the only two samples then available, and would not be apparent without the availability of numerous large populations.

De Bruijn et al. (1970) considered the mesoflexid to be derived, because in comparing the only two *Trischizolagus* samples then known, Maritsa and Malusteni-Beresti, the individuals from the younger fauna more frequently showed a mesoflexid. Now, with sev-

eral samples distributed through time, the opposite polarity seems more justified. Derived taxa are often, but certainly not always, younger than primitive taxa. Perhaps the Romanian *T. dumitrescuae* is a species that retained the primitive mesoflexid morphology although the earlier Greek *T. maritsae* showed frequent suppression of it.

LEPORINAE, INDETERMINATE

REFERRED MATERIAL: AMNH 116243, proximal half of right humerus.

LOCALITY AND HORIZON: Kholobolchi Nor C; strata assigned to the Khunuk Formation.

DESCRIPTION AND DISCUSSION: The humerus compares well with Lepus americanus in size and most features, but the head is oval in proximal view, unlike Lepus and Sylvilagus, which have round heads. It seems reasonable that the humerus could represent Trischizolagus sp.

ORDER PROBOSCIDEA ILLIGER, 1811

SUBORDER ELEPHANTOIDEA OSBORN, 1921

FAMILY, GENUS, AND SPECIES, INDETERMINATE

Serridentinus florescens, n. sp., Osborn, 1929:6. Ocalientinus (Serridentinus) florescens, Osborn, 1936:397.

Gomphotherium sp. or Platybelodon sp., Tobien, 1972:173.

REFERRED MATERIAL: AMNH 21615, fragmentary right lower second molar.

LOCALITY AND HORIZON: Kholobolchi Nor B; strata assigned to the Khunuk Formation.

Discussion: This specimen has been well described by Osborn (1929, 1936) and Tobien (1972). It is in fact laterally crushed, and Tobien (1972) considered it insufficient for specific level identification (or diagnosis). He thus did not recognize Osborn's Serridentinus florescens, which was based only on AMNH 21615, and stated that the tooth probably represented a species of Gomphotherium, although Platybelodon could not be ruled out. Presently, Tobien (personal commun.) regards AMNH 21615 as indeterminate, but possibly representative of the eastern Asiatic late Neogene genus Sinomastodon Tobien et al. (1986).

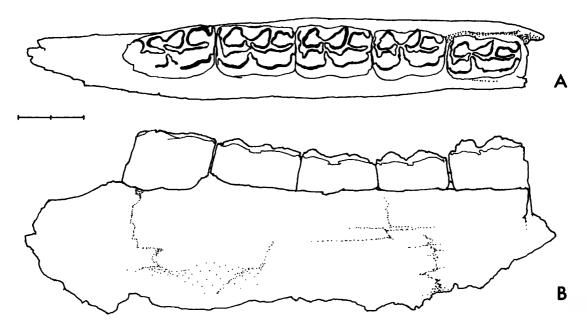


Fig. 4. Occlusal (A) and labial (B) views of left dentary, AMNH 116232, "Hipparion" houseness.

ORDER PERISSODACTYLA OWEN, 1848 SUBORDER HIPPOMORPHA WOOD, 1937 FAMILY EQUIDAE STEINMANN AND DODERLEIN, 1890

"Hipparion" housenesse
Teilhard de Chardin and Young, 1931

LECTOTYPE: RV 31031, left mandible fragment with P₃-M₃ (Teilhard de Chardin and Young, 1931, p. 40, text fig. 14).

TYPE LOCALITY: Locality 1, Chingle Formation, China (also spelled "Jingle" or "Jinle").

GEOGRAPHIC RANGE AND AGE: China, early Pliocene to early Pleistocene (Jinglean to Nihewanian); the Mongolian People's Republic, late Miocene through Pliocene.

DIAGNOSIS (after Qiu et al., 1980): Skull medium to large size, lacking preorbital fossa; nasal notch incised to the mesostyle of P²; supraorbital and infraorbital foramina large; zygomatic arch strongly built; incisors with longitudinal grooves on both lingual and labial sides and with a tendency to develop lingual pillars; maxillary cheek teeth in middle adult wear show moderately complex fossette plications, pli caballins short and usually double, protocones large, virtually

triangular shaped, elongated, and lingually flattened; lower canine placed very close to I_3 ; P_2 anterostylid elongate, lower cheek teeth in middle adult wear have usually strongly expressed protostylids, deep and broadly U-shaped linguaflexids, elongate ectostylids with simple borders, metaflexids square shaped on premolars and slightly elongate on molars, and finally, metaconids and metastylids with persistently strongly angled interior margins, except on P_2 .

REFERRED SPECIMENS: AMNH 116232, old adult left mandible fragment with P₂–M₂; AMNH 116233, distal metacarpal fragment; AMNH 116234, proximal metacarpal fragment; AMNH 116235, 2nd and 3rd phalanx III; AMNH 116236, distal radius fragment; AMNH 116237, distal humerus fragment; AMNH 116238 and AMNH 116239, two distal tibia fragments.

LOCALITY AND HORIZON: AMNH 116232 from Kholobolchi Nor A; precise locality information for other specimens not recorded; all specimens from Khunuk Formation (Granger, 1925, fieldnotes).

DESCRIPTION: There are nine hipparionine specimens present in the AMNH Kholobolchi Nor collection. Included are a fragmentary left mandible, a proximal metacarpal III

TABLE 1

Measurements on the Kholobolchi Nor, Chinglo, and Matzekou Hipparionine Mandibular

Cheek Teeth (mm)^a

| Element | Length | Width | P ₂ Met | Ect Flx | Pli | Pro Std | Ling Flx | Mec Mstd | Ent Mor | Ent Bor | Met Mor |
|------------------|--------|-------|-----------------------|------------|-----|------------|-------------|-------------|------------|------------|------------|
| AMNH 116 | 232 | - | | | | · | | | | | |
| P_2 | e31.5 | 16.9 | _ | _ | _ | ? | * | -/- | + | _ | _ |
| P_3 | 24.7 | 16.4 | | _ | _ | + | * | -/- | + | _ | |
| P ₄ | 23.0 | 15.7 | | _ | _ | + | * | -/- | + | _ | -/+ |
| \mathbf{M}_1 | 21.8 | 14.9 | | + | _ | + | * | -/- | +/- | _ | -/+ |
| M_2 | e23.0 | e14.0 | | _ | _ | + | * | -/- | + | _ | -/+ |
| P_{2-4} | 79.4 | | | | | | | | | | |
| RV 31031 | | | | | | | | | | | |
| P ₃ | 23.5 | 17.0 | | | | | | | + | _ | _ |
| P ₄ | 24.0 | 17.0 | | | | | | | + | _ | _ |
| \mathbf{M}_1 | 21.0 | 16.5 | | | | | | | +/- | _ | -/+ |
| M_2 | 23.5 | 16.0 | | | | | | | +/- | _ | -/+ |
| M_3 | 24.0 | 15.0 | | | | | | | +/- | _ | -/+ |
| THP.10508 | | | | | | | | | | | |
| I_2 | 12.0 | 11.8 | | | | | | | | | |
| I ₃ | 12.2 | 9.2 | | | | | | | | | |
| Č | 12.0 | 9.4 | | | | | | | | | |
| P_2 | 29.5 | 12.8 | | _ | ?- | _ | + | -/- | | | |
| P_3^- | 25.0 | 15.0 | | _ | ?- | _ | * | -/- | | | |
| P ₄ | 24.0 | 15.4 | | _ | ?- | _ | * | -/- | | | |
| \mathbf{M}_1 | 22.2 | 14.3 | | + | ?- | | * | -/- | | | |
| M_2 | 22.5 | 14.3 | | + | ?- | _ | * | -/- | | | |
| M_3 | 28.0 | 14.0 | | + | ?- | _ | * | -/- | | | |
| P_2-M_3 | 157.0 | | | | | | | | | | |
| P ₂₋₄ | 86.0 | | | | | | | | | | |
| M_{1-3} | 70.0 | | | | | | | | | | |

a Abbreviations: e, estimated; P₂ Met, rounded (+) or elongated (-) metastylid; Ect Flx, ectoflexid separates (+) or does not separate (-) metaconid and metastylid; Pli, pli caballinid is complex (+), rudimentary to single (*), or absent (-); Pro Std, protostylid is present (+) or rudimentary to single (*); Ling Flx, linguaflexid between metaconid and metastylid is shallow (+), U-shaped (*), or V-shaped (-); Mec Mstd, metaconid/metastylid shape is rounded (+) or angular (-); Ent Mor, entoflexid elongate (+) or short (-); Ent Bor, entoflexid border complex (+) or simple (-); Met Mor, metaflexid squared (+) or elongated and narrow (-).

fragment, a distal metacarpal III fragment, a 2nd and 3rd phalanx III, and fragments of two distal tibiae, a distal radius, and a distal humerus. The specimens are not associated and there is no evidence that they all came from precisely the same site.

AMNH 116232 is a fragmentary left mandible with P_2 – M_2 (fig. 4, tables 1, 2). P_2 has a broken anterostylid, but would appear to have been elongated. Ectoflexids are shallow on the premolars, somewhat deeper on M_2 . There are no pli caballinids or traces of enamel complexity. Protostylids are present on the anterobuccal margin of P_3 – M_2 . Linguaflexids

are shallow on P₂, but are deeper, yet broadly open and U-shaped on the remaining cheek teeth. Metaconids and metastylids have angular contours. Metaflexids are generally rectangular shaped and longer than wide. Entoflexids are extremely elongated anteroposteriorly and narrow transversely.

The metacarpals (fig. 5) indicate a medium size hipparionine and compare well in their size with the mandible described above (see measurements in tables 3 and 4 and refer to Bernor, 1985). The proximal metacarpal, AMNH 116234, has a facet for articulation with the magnum and hamate oriented at

| | | | TA | BLE 2 | | | | | |
|-----------------|--------|--------|---------|----------------|----------------|--------|---------|---------|--------------------|
| Measurements of | on Hip | parion | ine Maı | ndibula | r Che | ek Tee | th fron | ı Hsi C | huang ^a |
| | Can | Snt | Ment | P ₂ | P ₂ | Ect | | Pro | Ling |

| Element | Length | Width | Can Pos | Snt Lng | Ment For | P ₂ Ant | P ₂ Met | Ect Flx | Pli | Pro Std | Ling Flx | Mec Mstd |
|---------------------|-------------|-------|------------|------------|-------------|-----------------------|-----------------------|------------|-----|------------|-------------|-------------|
| AMNH 111 | AMNH 111820 | | | | | | | | | | | |
| \mathbf{I}_{1} | 14.7 | 13.8 | + | + | * | | | | | | | |
| I_2 | 15.7 | 13.1 | | | | | | | | | | |
| | 15.2 | 11.0 | | | | | | | | | | |
| I ₃ C | 5.6 | 6.0 | | | | | | | | | | |
| P_2 | 33.7 | 16.9 | | | | + | + | _ | _ | _ | + | +/- |
| P_3 | 28.7 | 16.8 | | | | | | _ | _ | _ | * | -/- |
| P_4 | 25.0 | 15.4 | | | | | | _ | _ | _ | * | -/- |
| \mathbf{M}_1 | 25.1 | 17.2 | | | | | | + | _ | _ | * | -/- |
| M_2 | 25.6 | 15.9 | | | | | | + | - | _ | * | -/- |
| M_3 | 28.5 | 12.8 | | | | | | _ | - | _ | * | -/- |
| P_2-M_3 | 164.5 | | | | | | | | | | | |
| P_{2-4} | 88.5 | | | | | | | | | | | |
| M_{1-3} | 79.2 | | | | | | | | | | | |
| AMNH 110 | 5245 | | | | | | | | | | | |
| P_2 | 30.5 | 13.8 | | | | _ | + | _ | _ | | +/* | +/- |
| P_3^- | 25.6 | 13.9 | | | | | | _ | _ | + | * | _ |
| P ₄ | 25.2 | 13.7 | | | | | | _ | _ | + | * | _ |
| $\mathbf{M_1}$ | 22.0 | 11.7 | | | | | | + | _ | + | * | _ |
| M_2 | 22.9 | 11.5 | | | | | | + | _ | + | * | _ |
| M_3 | 28.0 | 10.9 | | | | | | + | _ | + | * | _ |
| $P_{2}-M_{3}$ | 150.4 | | | | | | | | | | | |
| P ₂₋₄ | 79.4 | | | | | | | | | | | |
| M_{1-3} | 71.9 | | | | | | | | | | | |

^a Abbreviations as in table 1, plus: Can Pos, canine positioned closer to I_3 than P_2 (+) or closer to P_2 than I_3 (-); Snt Lng, relative snout length, P_2 – I_1 length greater than P_2 – M_3 length (+) or less than P_2 – M_3 length (-); Ment For, mental foramen positioned closer to I_3 than P_2 (+) or closer to P_2 than P_3 (-); P_2 Ant, anterostylid symbols as for P_2 Met.

131°. The distal metacarpal shows only a moderately prominent sagittal keel, and is otherwise typical for hipparionine horses. The remaining postcranial elements are generally compatible in their size with the metapodials and their size falls within, or close to, the lectotype assemblage of "H." houfenense (see table 3).

DISCUSSION: The mandibular specimen that we report here, AMNH 116232, has a number of distinctive morphological characters, which we believe to be significant at the species level, including: prominent protostylids on the cheek teeth, angular shaped metaconids and metastylids (except metaconid on P₂), linguaflexid deep and broadly U-shaped (especially the molar teeth), and entoflexids elongate and narrow. The AMNH mandible compares very closely in both size and mor-

phology with the lectotype, RV 31031, a mandible fragment with P₃-M₃. Likewise, the Kholobolchi postcranial fragments compare closely in size to the lectotype assemblage of "Hipparion" housenesse (Teilhard de Chardin and Young, 1931, p. 50, their text fig. 14; see our tables 3 and 4).

Both the lectotype specimen and the Kholobolchi Nor mandible show a very close resemblance to an associated skull and lower jaw referred by Qiu et al. (1980) to *Hipparion housenense*. This specimen, THP.10508, was collected from Loc. 26, Matzekou, Baihai Village, Shanxi. The authors reported that (1) the skull represents a medium to large size hipparionine lacking a preorbital fossa, (2) maxillary cheek teeth display moderate complexity of the pre- and postfossettes, and have triangular shaped, elongated, and lingually

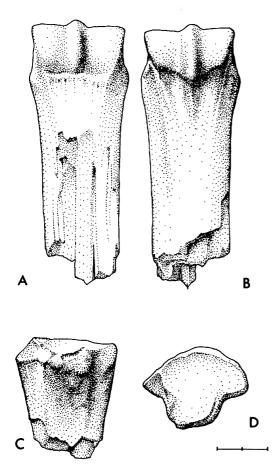


Fig. 5. Posterior (A) and anterior (B) views of distal metacarpal, AMNH 116233; posterior (C) and articular (D) views of proximal metacarpal, AMNH 116234; both "Hipparion" housenesse.

flattened protocones, and (3) pli caballins are single or double. The maxillary cheek teeth have deeply incised hypoglyphs. All incisors have deep longitudinal grooves on both the lingual and labial sides, and lower incisors bear a prominent lingual pillar. The M₃'s of RV 31031 and THP.10508 are distinctive in that their hypoconulids have a double enamel-loop.

The American Museum Frick collection contains specimens resembling "Hipparion" houseness, including a fragmentary mandible (AMNH 116245) and a skull associated with mandible (AMNH 111820) from the Nihewan age locality of Hsia Chuang, 10 mi south of Shouyang. This locality, as well as other Nihewan equivalents, produces specimens of a derived hipparionine, Proboscidip-

TABLE 3

Comparison of Postcranial Dimensions for the Hypodigm of "Hipparion" houfenense^a and the Kholobolchi Nor Hipparionine Assemblage

| ı, mm | Kholobolchi Nor sample, mm |
|---------|--|
| 74–57 | AMNH 116238:63.7 |
| | |
| 100 | |
| 64 | |
| | |
| 55–267 | |
| 46-43 | |
| 32-26.5 | |
| 70 | |
| 43 | |
| 30 | |
| 38 | |
| 48 | AMNH 116235:42.4 |
| 46.5 | 39.0 |
| 38.0 | 33.6 |
| 41.0 | 36.0 |
| th 51.0 | AMNH 116235: NM |
| 66.5 | NM |
| ith | AMNH 116237:62.5 |
| | AMNH 116236: NM |
| | 74–57 100 64 55–267 46–43 32–26.5 70 43 30 38 48 46.5 38.0 41.0 66.5 |

^a After Teilhard de Chardin and Young, 1931:50. NM = not measurable.

parion sinense, and Equus sanmanensis. AMNH 116245 is a mandible with right and left P₂-M₃ lacking its anterior dentition and ascending rami. All features of the metaconid, metastylid, metaflexid, entoflexid, linguaflexid, ectoflexid, protostylids, and M₃ double hypoconulid are virtually identical to those of older "Hipparion" housenesse. AMNH 111820 also compares closely with the above described hypodigm except that it is larger and lacks protostylids, possibly due to breakage of the lower cheek tooth labial margins. We believe that this Nihewan age horse should presently be considered as "Hipparion" aff. "H." housenesse in view of its apparently larger size (tables 1, 2) and longer snout length than the Chinglo and Kholobolchi Nor materials. Its size alone would suggest that it is probably a distinct species.

Gromova (1952) suggested that "Hipparion" housenesse was a plausible intermediate form linking Hipparion with Proboscidippar-

TABLE 4
Kholobolchi Nor Hipparionine Metacarpal Measurements (mm)^a

| | | Specimen | | | | |
|-----|--|----------|---------------------------------|--|--|--|
| | Measurement | | AMNH 116234, proximal MC III | | | |
| 1. | Maximum length. | | | | | |
| 2. | Length from proximomedial surface to the distornedial condylar surface. | | | | | |
| 3. | Middiaphysial mediolateral width. | 29.5 | | | | |
| 4. | Middiaphysial anteroposterior width. | 19.7 | | | | |
| 5. | Maximum mediolateral width of proximal articular surface. | | | | | |
| 6. | Maximum dorsoventral height of proximal articular surface. | | | | | |
| 7. | Distance from hamate/magnum articular ridge to lateralmost aspect of | | | | | |
| | the magnum articular facet. | | 33.7 | | | |
| 8. | Maximum width of articular facet for the hamate at the lateral peripheral | | | | | |
| | border. | | 11.9 | | | |
| 9. | Anteroposterior length of facet for the proximolateral facet of MC II. | | 6.9 | | | |
| 10. | Distal mediolateral width across the epicondyles. | 39.0 | | | | |
| 11. | Distal mediolateral width across the condyles. | 35.5 | | | | |
| 12. | Anteroposterior width of distal sagittal keel. | 29.7 | | | | |
| 13. | Anteroposterior length of distal condyles just lateral to the sagittal keel. | 24.5 | | | | |
| 14. | Anteroposterior length of lateralmost aspect of distal condyles. | 25.0 | | | | |

^a See Bernor (1985) for further explanation on measuring technique.

ion. More recently, Qiu et al. (1980) suggested that "H." housenesse shares many characters with the Baodean age species "H." hippidiodum, namely absence of a preorbital fossa, rather long muzzle, similar form of the nasal notch, weak cheek tooth fossette plications, and very simple pli caballins on the upper cheek teeth. These authors considered "H." hippidiodum to be a possible ancestor of "H." houfenense, but Qiu (personal commun.) now rejects this. Recently, MacFadden (1984, pp. 187–188, fig. 151) suggested that "H." housenesse may have been derived from a species of the North American Neohipparion lineage, and referred the Chinese skull AMNH 111820 to "Hipparion (Neohipparion)" houfenense. He stressed that Asiatic collections need further analysis.

The Uppsala Chinese assemblage contains the lectotype of "H." hippidiodum (PMU 3819). The lectotype and hypodigm of "H." hippidiodum (sensu Bernor and Qiu, in prep.) differs from "H." housense in having simpler plications of the pre- and postfossettes, persistently single pli caballins, hypoglyphs less deeply incised, protocones rounded rather than triangular shaped and elongated with a flattened lingual margin. The different constellations of upper cheek tooth characters

exhibited by "H." hippidiodum and "H." housenesse potentially falsify Qiu et al.'s (1980) hypothesis of ancestral-descendent relationship for these species. Furthermore, the slight nasal incision and loss of the preorbital fossa are characters found in multiple lineages of New and Old World hipparionines (Bernor and Hussain, 1985; Bernor, 1986) and are a further source of suspicion about these relationships.

The phylogenetic relationships of "Hipparion" housenesse are currently under investigation by Bernor. Review of the American Museum Frick equid collection reveals a number of features shared by "Hipparion" housenesse and the older (ca. 8 Ma) Middle Siwalik species "Cormohipparion" (Sivalhippus) perimense (Bernor and Hussain, 1985). "C." (S.) perimense has (1) triangular shaped and lingually flattened protocones, although not as elongated and strongly triangular as in "H." houfenense, (2) strongly developed protostylids on all P2's through M2's, (3) metaconids and metastylids showing a tendency for angular shape, (4) linguaflexids deeply U-shaped, and (5) hypoconulid with a distinct double enamel loop on M₃. "Cormohipparion" (Sivalhippus) perimense has a reduced preorbital fossa placed well anterior on the face and would be less derived than "H." housenesse, assuming a trend toward loss of the fossa in this clade.

These lines of evidence suggest the possibility of an autochthonous South Asian origin of the "Hipparion" housenesse clade, and if corroborated would falsify the hypothesis (in MacFadden, 1984) of its separate North American origin and migration into Asia ca. 6 Ma. Moreover, Bernor and Hussain (1985) have suggested similar polarities in character states of the preorbital fossa and maxillary cheek teeth for "C." (S.) perimense and the late Miocene East African equid, "H." turkanense (Hooijer and Maglio, 1974). The possibility of close phylogenetic relationship between the Siwalik horse "C." (S.) perimense and various Asian and Subsaharan African late Miocene and Pliocene age hipparionine taxa would have major implications for interpreting the late Neogene intercontinental distribution of horse groups.

SUBORDER CERATOMORPHA WOOD, 1937
FAMILY RHINOCEROTIDAE OWEN, 1845
Chilotherium sp.

REFERRED MATERIAL: AMNH 116240, lingual two-thirds of a left DP².

LOCALITY AND HORIZON: Kholobolchi Nor C: strata assigned to the Khunuk Formation.

DESCRIPTION AND DISCUSSION: This deciduous premolar is low crowned, 25 mm long, and slightly worn. The metaloph and protoloph are strongly angled, and the metaloph and (evidently) the protoloph are bifurcated at their labial ends. A strong cingulum includes a tricuspid lingual pillar posterior to the protocone, but the cingulum weakens next to both the hypocone and the protocone. AMNH 116240 is the same size as Chilotherium intermedium from Pakistan (Heissig, 1972), but more resembles species from China in strength of the cingulum and bifurcation of the metaloph. The specimen compares well with *Chilotherium* studied by Ringström (1924), except that the metaloph and protoloph appear to be rather more oblique in AMNH 116240. The obliquity is comparable, however, in the large species Chilotherium tianzhuense Zheng (1982). The Kholobolchi Nor specimen is about the same

size as *Chilotherium tanggulaense* Zheng (1980). AMNH 116240 shows greatest affinity with Mio-Pliocene *Chilotherium* from China, but is not clearly assignable to a known species at present.

ORDER ARTIODACTYLA OWEN, 1848
FAMILY BOVIDAE GRAY, 1855
Oioceros Gaillard, 1902

"Oioceros" sp.

REFERRED MATERIAL: AMNH 21616, left horn core and partial orbital region.

LOCALITY AND HORIZON: Kholobolchi Nor C; strata assigned to the Khunuk Formation.

DESCRIPTION: The Kholobolchi Nor fauna includes a left bovid horn core with partial orbit and cranium intact (fig. 6). The horn is relatively short, having a maximum height, as measured along its anterior midline, of 84 mm. The horn core has longitudinal furrows from the top of the pedicle to its tip, some of which run for most of the length of the core. There is no keel, but the horn has a slight counterclockwise torsion from the base upward. AMNH 21616 tapers gradually in its transverse diameter, measuring 22 mm at its base, 17.1 mm at its midline, and 9 mm at its apex, where only the tip is lacking. It is nearly circular in cross section. In anterior view the horn core is concave anterolaterally so that the tip is lateral to the midline of the specimen.

DISCUSSION: During a visit to the AMNH in 1976, Dr. E. Vrba identified AMNH 21616 as Oioceros. Although the specimen shows a reasonable similarity to the Tung Gur Oioceros (Oioceros(?) grangeri and Oioceros(?) noverca [sic], Pilgrim, 1934), it is distinctly longer and has a lesser torsion. We refer to the Kholobolchi Nor specimen as "Oioceros" sp. because its morphology, and the morphology of the Tung Gur species, differs greatly from that of the late Miocene species O. rothi and O. atropatenes from Pikermi and Maragheh (see Gaillard, 1902; Pilgrim, 1934; Heintz, 1963; Solounias, 1981; Whybrow et al., 1982; Bernor, 1986). The consensus is that horn cores sharing counterclockwise torsion represent more than one genus and perhaps more than one major group, but that material is in general too scarce for a comprehensive revision (see Gabunia, 1973; Solounias, 1981; Thomas, 1983; Bouvrain and de Bonis, 1985). Dr. Nikos Solounias (personal commun.) points out that without better material of these simple-horned bovines (little or no torsion, nearly circular outline), rupicaprine affinity cannot be ruled out.

"Oioceros" is present elsewhere in Mongolia (Dmitrieva, 1977), and occurs 25 mi to the southeast of Kholobolchi Nor at Hung Kureh. Horn cores from that locality in the Central Asiatic Expedition collection of the AMNH are distinctly more twisted and compressed than those of either Tung Gur or Kholobolchi Nor, but are still much less derived than O. atropatenes.

AGE OF THE KHUNUK FORMATION

The Khunuk Formation, as it is exposed in three areas, appears to be considerably older than previously believed. Early workers had considered the formation to be Pleistocene in age, based on a field identification of AMNH 116232 as Equus. This led to mistaken identifications on other specimens in the sample from Kholobolchi Nor. [Equus is now known to appear in the late Pliocene in Asia (ca. 2.5 Ma, Lindsay et al., 1980)]. In reality the horse jaw is a "Hipparion." The few fossils from Kholobolchi Nor come from scattered localities (sites A, B, C, fig. 1), and possibly differ somewhat temporally, yet they provide limits on the age of the formation. Thus, we conclude that sediments of the Khunuk Formation were deposited during the early Pliocene and/or the late Miocene. The Trischizolagus species present in Mongolia (site C) is not distinguishable from that of Pul-e Charkhi, Afghanistan, based on specimens presently available. Sen (1983) presents strong arguments for Pul-e Charkhi's early Pliocene age. The hipparionine (site A) compares favorably with the early Pliocene to early Pleistocene age "Hipparion" houfenense from China, although it is somewhat smaller in size. Perhaps the Kholobolchi Nor equid can be shown to be closest to earlier "H." housenesse from northwestern Mongolia, dated as latest Miocene (late Epoch 5, about 5.5 Ma; Pevzner et al., 1982).

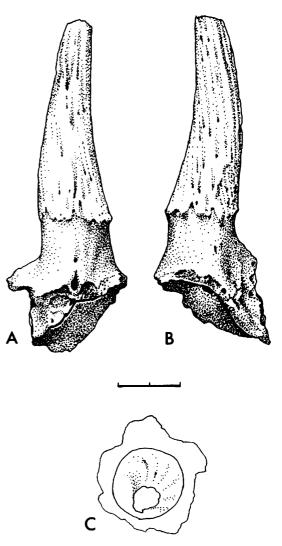


Fig. 6. Medial (A), lateral (B), and apical (C) views of horn core AMNH 21616, "Oioceros" sp. The apical view shows the degree and sense of torsion and that the tip corkscrews off center with respect to the base.

Also from site C in the Khunuk Formation is the bovid "Oioceros," which is common in middle and late Miocene deposits throughout eastern Asia. The Kholobolchi Nor "Oioceros" horn core, AMNH 21616, resembles "Oioceros" from the middle Miocene Tung Gur sample of Inner Mongolia, but differs in size and torsion. Without better material, this faunal element is not very useful temporally. Tentative identifications for the fragmentary proboscidean and rhinocerotid fossils are

consistent with a late Neogene age. As an assemblage, the known faunal elements suggest an age very near the Miocene-Pliocene epoch limit for the Kholobolchi Nor exposures of the Khunuk Formation.

In conclusion, the Kholobolchi Nor fossil mammal collection of the 1925 Central Asiatic Expedition includes jaw fragments of a leporid and a hipparionine horse that are conspecific with fossils from early Pliocene or late Miocene deposits elsewhere. These specimens, plus a bovid, a proboscidean, and a rhinocerotid, argue for a Mio-Pliocene age for at least part of the Khunuk Formation. The foregoing demonstrates that these strata are comparable in age to the better known Hung Kureh "Hipparion beds" to the southeast and the Hyargas Nuur Formation in northwestern Mongolia (see Pevzner et al., 1982). It is plausible that all of the late Neogene sediments on the north flank of the Altai Mountains have a related tectonic origin. Collectively, these strata probably will prove to yield late Tertiary assemblages that will complement the important reference faunas of China to the extent that the temporal and geographic limits of Asian Miocene and Pliocene mammalian provincial ages will become better documented.

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